Vol. 653: 167–179, 2020
https://doi.org/10.3354/meps13488

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 29[§]

Environmental conditions are poor predictors of immature white shark *Carcharodon carcharias* occurrences on coastal beaches of eastern Australia

Julia L. Y. Spaet[1,2,*], Andrea Manica[1], Craig P. Brand[3], Christopher Gallen[4], Paul A. Butcher[2,3]

[1]Evolutionary Ecology Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK
[2]National Marine Science Centre, Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Coffs Harbour, New South Wales 2450, Australia
[3]Fisheries NSW, NSW Department of Primary Industries, National Marine Science Centre, Coffs Harbour, New South Wales 2450, Australia
[4]Fisheries NSW, NSW Department of Primary Industries, Port Stephens Fisheries Institute, Nelson Bay, New South Wales 2315, Australia

ABSTRACT: Understanding and predicting the distribution of organisms in heterogeneous environments is a fundamental ecological question and a requirement for sound management. To implement effective conservation strategies for white shark *Carcharodon carcharias* populations, it is imperative to define drivers of their movement and occurrence patterns and to protect critical habitats. Here, we acoustically tagged 444 immature white sharks and monitored their presence in relation to environmental factors over a 3 yr period (2016–2019) using an array of 21 iridium satellite-linked (VR4G) receivers spread along the coast of New South Wales, Australia. Results of generalized additive models showed that all tested predictors (month, time of day, water temperature, tidal height, swell height, lunar phase) had a significant effect on shark occurrence. However, collectively, these predictors only explained 1.8% of deviance, suggesting that statistical significance may be rooted in the large sample size rather than biological importance. On the other hand, receiver location, which captures geographic fidelity and local conditions not captured by the aforementioned environmental variables, explained a sizeable 17.3% of deviance. Sharks tracked in this study hence appear to be tolerant to episodic changes in environmental conditions, and movement patterns are likely related to currently undetermined, location-specific habitat characteristics or biological components, such as local currents, prey availability or competition. Importantly, we show that performance of VR4G receivers can be strongly affected by local environmental conditions, and provide an example of how a lack of range test controls can lead to misinterpretation and erroneous conclusions of acoustic detection data.

KEY WORDS: Acoustic telemetry · New South Wales · Generalized additive model · GAM · Range test · Receiver performance · Seasonality · Spatial · Temporal

1. INTRODUCTION

Variation in the spatial distribution of wild animals is largely determined by shifts in habitat use of individuals. The habitat of an animal is the natural environment in which it normally lives and is defined by numerous, co-varying abiotic and biotic factors (Partridge 1978). Most animals actively select appropriate habitat through movements in response to physical (e.g. temperature and sunlight) and biological conditions (e.g. food availability and presence of conspecifics) (Nathan et al. 2008). Vagile organisms, e.g.

*Corresponding author: jlys3@cam.ac.uk

[§]Corrections were made after publication. For details see www.int-res.com/abstracts/meps/v653/c_167-179
This corrected version: October 30, 2020

Publisher: Inter-Research · www.int-res.com

larger shark species, typically only frequent coastal waters when conditions are favourable and move away when confronted with adverse conditions (see Schlaff et al. 2014 for a review). The main drivers of these movements are commonly species- and context-specific (Udyawer et al. 2013, Wintner & Kerwath 2018) and can include factors as diverse as water temperature (e.g. Heupel et al. 2007, Werry et al. 2018); tidal cycle (e.g. Ackerman et al. 2000, Carlisle & Starr 2010); barometric pressure (e.g. Matich & Heithaus 2012, Udyawer et al. 2013); rainfall (Werry et al. 2018); and pH (Ortega et al. 2009). The influence of these drivers on individuals of the same species can also be greatly affected by sex, ontogenetic stage, geographic location and season (Schlaff et al. 2014). In light of the growing anthropogenic threats faced by marine predators worldwide, such as alterations of coastal habitat, pollution and climate change, understanding how these organisms respond to rapid environmental change is becoming increasingly important.

Coastal habitats along the Australian east coast are regularly frequented by juvenile and sub-adult (hereafter referred to as immature) white sharks *Carcharodon carcharias* (Linnaeus 1758) which, except for occasional across-ocean excursions (Bruce et al. 2019, Spaet et al. 2020), primarily move among a relatively small number of interconnected habitats and the 120 m depth contour (Bruce et al. 2006, Werry et al. 2012). These animals belong to a single, relatively small population (ca. 2500–6750 individuals) inhabiting the waters surrounding eastern Australia and New Zealand (Hillary et al. 2018), hereafter referred to as eastern Australasian white sharks. Fine-scale patterns and site fidelity to foraging, aggregation and nursery areas (Robbins 2007, Bruce & Bradford 2012, Spaet et al. 2020) make the juvenile subset of this population particularly vulnerable to potential threats, such as incidental capture in recreational and commercial fisheries (Bruce & Bradford 2012, Lowe et al. 2012, Oñate-González et al. 2017), capture in bather protection programmes (Lee et al. 2018, Tate et al. 2019) habitat destruction, pollution (Suchanek 1994, Mull et al. 2013) and climate change (Chin & Kyne 2007). Globally, white sharks are listed as Vulnerable based on International Union for Conservation of Nature (IUCN) Red List criteria (Rigby et al. 2019), and have been afforded protection under various national jurisdictions and international treaties, such as listing in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and the Convention on the Conservation of Migratory Species of Wild Animals (CMS). This has fostered wide-ranging research and conservation efforts over much of their global distribution (Huveneers et al. 2018). White sharks are listed as threatened in Australia's Environment Protection and Biodiversity Conservation Act of 1999, and conservation objectives at a national level have been formulated under a national recovery plan (Department of Sustainability, Environment, Water, Population and Communities 2013). A key priority of research under this plan is the characterisation of patterns and drivers of spatial and temporal variability in habitat occupancy. Elucidating the mechanisms behind white shark distribution and movements is a prerequisite to the implementation of ecologically sound conservation strategies (Southall et al. 2006, Certain et al. 2007) and has recently also been identified as one of the top 10 research priorities for this species globally (Huveneers et al. 2018).

Evidence of the effects of abiotic factors on white shark movements and temporal residency has been reported from various locations across their range. For most abiotic factors, there are observed linkages to white shark presence and behaviour; however, these appear to be highly region- and context-specific, and hence cannot be expanded to the species as a whole. For example, in response to new moon, white shark presence increased at 2 beaches in South Africa and at a seal colony in California (Pyle et al. 1996, Weltz et al. 2013). Similarly, white shark catch rates increased during the new moon in shark control programmes along the Australian east coast (Werry et al. 2012, Lee et al. 2018). In contrast, lunar phase was not a significant predictor of white shark catch rates in a bather-protection programme along the east coast of South Africa (Wintner & Kerwath 2018).

The most widely studied abiotic factor in relation to white shark presence and distribution is temperature. Variations in water temperature have been linked to white shark abundance and catch rates along the east coasts of Australia and South Africa, and the Farallon Islands, California (Pyle et al. 1996, Towner et al. 2013, Weltz et al. 2013, Lee et al. 2018, Wintner & Kerwath 2018). However, whether temperature is directly influencing white shark presence by affecting thermoregulation or indirectly by affecting prey distribution and abundance remains unclear. In addition to temperature and lunar phase, tidal height and wind speed also appear to play a role in the presence and behaviour of white sharks, although results across studies are inconsistent (Pyle et al. 1996, Robbins 2007, Weltz et al. 2013).

Given the described importance of environmental drivers in the distribution and movements of white sharks and the susceptibility of the eastern Australasian population to habitat modification (Depart-

ment of Sustainability, Environment, Water, Population and Communities 2013), we explored a range of environmental and temporal variables that could influence the occurrence of immature white sharks along the coast of New South Wales (NSW), eastern Australia. We used a 3 yr (2016–2019) acoustic telemetry dataset of 444 white sharks tagged in eastern Australia to: (1) determine the seasonal and diurnal variability in white shark occurrence; (2) model the relative influence of month, time of day, water temperature, tidal height, swell height and lunar phase on their presence; and (3) determine the impact of these variables on receiver performance by conducting range test experiments where possible. A better understanding of how these environmental factors affect site fidelity and movement dynamics is critical to forecast potential shifts in these traits under rapid environmental change, and will ultimately enhance our ability to predict where and when immature white sharks occur along the Australian east coast.

2. MATERIALS AND METHODS

2.1. Tagging

A total of 444 white sharks were tagged with Vemco V16-6L acoustic transmitters (Innovasea Marine Systems) with transmission intervals of 40–80 s and a 10 yr battery life. Transmitters were fitted to sharks between 26 August 2015 and 29 November 2019. Tagging operations were conducted in NSW coastal shelf waters between Byron Bay (28.76° S, 153.60° E) and Eden (37.36° S, 150.07° E) within ~0.5 km of the coast (Fig. 1). Most sharks (n = 406) were caught using Shark Management Alert in Real Time (SMART) drumlines (Guyomard et al. 2019), while others were either (1) visually located from a vessel or helicopter before being presented with a baited hook from a vessel (n = 14) (Harasti et al. 2017), (2) caught on surface-buoyed setlines (n = 7) (Bruce & Bradford 2012) or (3) incidentally caught in bather protection nets (n = 17) (Reid et al. 2011) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m653p167_supp.pdf). Following capture, sharks were brought alongside the boat and secured with a belly and tail rope. A total of 329 sharks were fitted with external transmitters by embedding nylon umbrella anchors into the dorsal musculature using applicator needles mounted on a hand-shaft. Another 99 sharks were internally tagged with transmitters surgically implanted into the abdominal cavity following the general procedure of Heupel et al. (2006b). Another 16 individuals were dual-acousti-

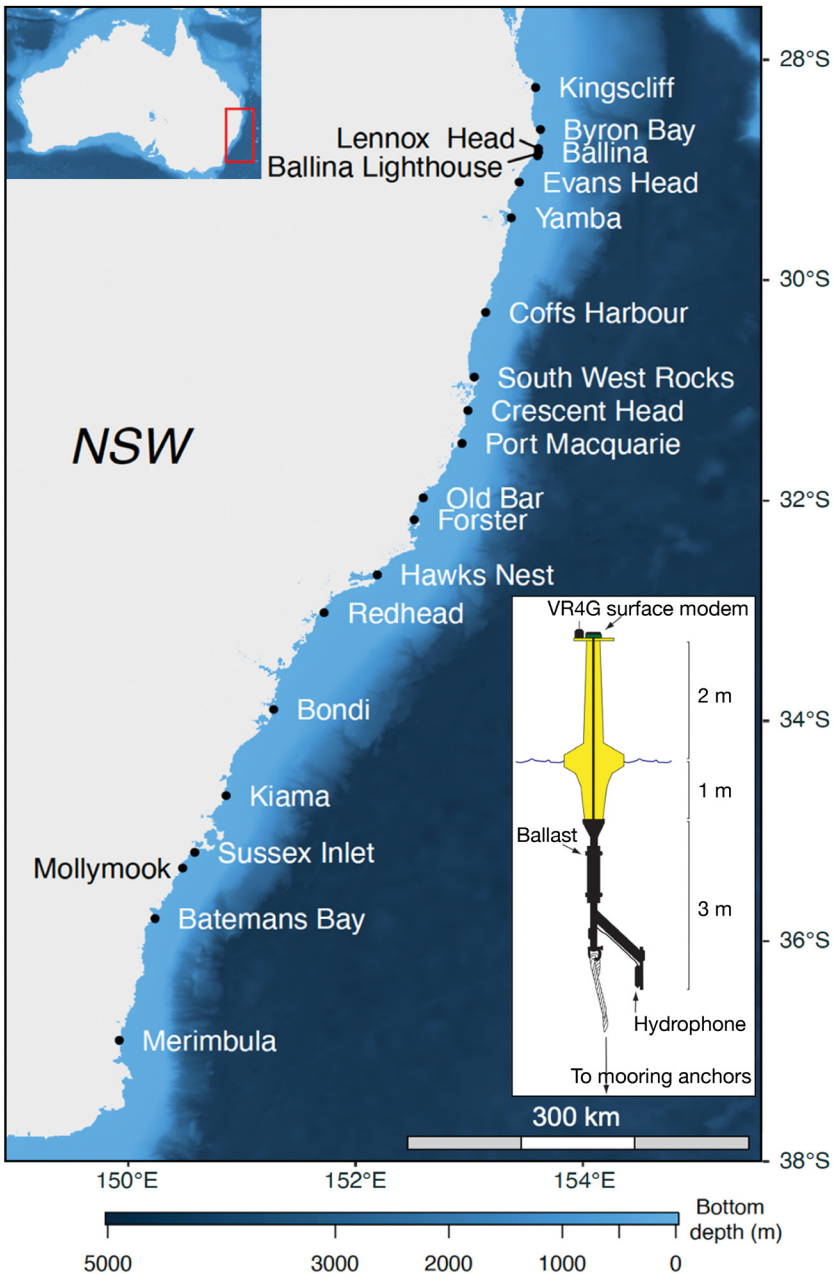

Fig. 1. Spatial distribution of acoustic VR4G receivers along the coast of New South Wales, Australia. Each location name corresponds to 1 VR4G receiver deployed at that location. Inset shows a schematic drawing of a VR4G receiver unit

cally tagged (with both internal and external transmitters). In addition, each shark was tagged with a uniquely numbered identification tag (spaghetti tag; Hallprint), which was inserted into the musculature at the base of the first dorsal fin for future visual identification. Between 07 September 2016 and 21 November 2019, 75 sharks were recaptured; of these, 7 individuals were recaptured twice and 3 individuals 3 times. Ten of the recaptured sharks that were originally tagged internally were fitted with an additional external transmitter during recapture. Prior to release, sharks were sexed, and fork length (FL) was measured to the nearest cm.

2.2. Range testing and receiver performance

Tagged sharks were monitored by an array of 21 iridium satellite-linked acoustic receivers (Vemco VR4-Global [VR4G]) (Fig. 1). VR4G moorings were deployed 500 m from shore in 6–16 m depth, with the hydrophone 4 m below the surface. The detection range of acoustic receivers can vary spatially and temporally based on a study system's specific properties (Medwin & Clay 1997). Based on limited available range testing data, the detection envelope of VR4G receivers appears to range between 200 and 500 m (Bradford et al. 2011, J. L. Y. Spaet & P. A. Butcher unpubl. data). Ideally, rigorous, long-term evaluations of detection range should be completed at all stages of a field study (Kessel et al. 2014). Due to logistical constraints, however, continuous range testing at all receiver locations was not feasible throughout the present study. Instead, 132 to 138 d range tests were conducted at 5 array-representative receivers toward the end of the study period. A full description of the range test experimental methods and results are presented in the Supplement (Text S1, Tables S2–S4, Figs. S1–S3).

2.3. Data analysis

2.3.1. Model development

Acoustic data were processed and analysed in the R Statistical Environment (R Core Team 2020). We used a generalized additive model (GAM) approach in the R package 'mgcv' (Wood 2017), with a binomial error structure to model presence/absences and smooth splines for environmental predictors, as most animals respond to the environment in a non-linear way (Aarts et al. 2008). To investigate relationships between environmental conditions and shark occurrences, we used presence–absence of each tagged shark per hour for each day of the study period as the response variable and chose 6 variables based on previously documented relationships with the movements of white sharks as explanatory variables (Pyle et al. 1996, Robbins 2007, Werry et al. 2012, Towner et al. 2013, Weltz et al. 2013, Lee et al. 2018, Wintner & Kerwath 2018): (1) month; (2) time of day; (3) temperature; (4) tidal height; (5) swell height; and (6) lunar phase (Table 1). Given that the sample unit in this study was an hourly bin, each predictor variable was selected to match this temporal scale as closely as possible. Environmental datasets were either collected *in situ* (water temperature) or obtained from external sources (e.g. swell height; Table 1). Ambient water temperature was recorded every 240 min by sentinel tags, which were attached either to the riser rope or the base of the VR4G leg, at about 1–2 m from the hydrophone and 2–4 m below the sea surface. Hourly mean tidal height and swell height data were obtained through Manly Hydraulics Laboratory, NSW (https://mhl.nsw.gov.au/). Lunar phase values were calculated using the 'moonAngle' function in the R package 'oce' (Kelley & Richards 2019), with 0 corresponding to new moon, 0.25 to the first quarter, 0.5 to full moon and 0.75 to the second quar-

Table 1. Summary of explanatory variables used during preliminary model selection. Details include unit of measure, source, degrees of freedom and spline-based techniques used for smoothing in the generalized additive model. AEST (AEDT): Australian Eastern Standard (Daylight) Time

Explanatory variable	Source	df	Spline
Temporal			
Time of day (h)	AEST/AEDT	24	Cyclic-cubic-regression
Month	Calendar	12	Cyclic-cubic-regression
Environmental			
Water temperature (°C)	Sentinel tags	1	Cubic-regression
Swell height (cm)	Manly Hydraulics Laboratory, NSW, Australia	1	Cubic-regression
Tidal height (cm)	Manly Hydraulics Laboratory, NSW, Australia	1	Cubic-regression
Lunar phase	R package 'oce'	0.01	Cyclic-cubic-regression

ter. Missing temperature, tidal and swell height values were interpolated using spline interpolation.

As tagging efforts were spread over ca. 52 mo, the duration an individual shark was tagged within the study period varied depending on the release date. If a shark was tagged before the start of the study period (i.e. 1 December 2016), the time at liberty of this shark was appointed to 1 December 2016 until 30 November 2019 (the end of the study period). If a shark was tagged after 1 December 2016, its time at liberty started on the date that it was tagged. For the 8 sharks that died during the study period, time at liberty ended on the date they died. For statistical analyses, we constructed a presence–absence matrix of 0s (no detection) and 1s (detection). Since the collected data were presence-only, we imputed absence data in order to use a binominal distribution. The presence/absence of each shark's time at liberty was apportioned into 1 h time bins (n = 24) for each receiver, following Lindholm et al. (2007). Multiple detections of the same individual within the same hour by the same receiver were treated as a single detection, whereby the first detection in the database was retained and the others discarded. Each detection was then assigned a '1' for that hour and individual, while a '0' was assigned when no detections were recorded in a given hour.

Given that model selection and inference in large datasets is computationally demanding, we used a random absence-selection procedure to reduce the high number of absences in the dataset (>124 700 000 absences vs. <7600 presences). Prevalence (i.e. the ratio between the number of presences and absences in the dataset) is believed to influence model performance when modelling the probability of occurrence of a species. Yet the effect of prevalence is significant only for datasets with extremely unbalanced samples (<0.01 and >0.99) (Jiménez-Valverde et al. 2009) and in particular does not affect model performance of GAMs (Barbet-Massin et al. 2012). Thus, for each shark, we included all presences, but subsampled the total available absences to use in the model by randomly selecting only 50 absences per presence. To test whether the random sample of absence records had an effect on model results, we first repeated the resampling exercise 5 times, which resulted in 5 datasets with the same presences but different absences. We then re-ran the final model for each of these datasets and compared the resulting model coefficients.

Since the receiver at Ballina Lighthouse (Fig. 1) was not deployed until 9 July 2017, this receiver was excluded from the modelling framework. To achieve a more even distribution of VR4G stations and to prevent the same individuals being detected by different receivers within the same time bin, the receiver at Lennox Head (Fig. 1) was also excluded, leaving 19 stations in the model. For each model, we included shark ID and receiver location as additive fixed effects to correct for pseudo-replication and account for unknown differences inherent to each location that are otherwise unaccounted for in our analysis. Whilst shark ID could have been treated as a random effect, mixed GAMs tend to be computationally expensive, and model selection would have been prohibitive (an analogous approach was taken by e.g. Clay et al. 2016 and Frankish et al. 2020). We ran all possible combinations of explanatory variables alongside the null model and calculated values of Akaike's information criterion corrected for small sample size (AICc) using the 'dredge' function in the R package 'MuMIn' (Bartoń 2019). To reduce overfitting during model construction, we initially set the maximum number of knots to four, and increased this number only if the model response curves did not match the raw data. Candidate models were ranked according to AICc and weight. We then individually assessed the importance of variables based on the proportion of deviance explained. For each variable, we calculated the predictive deviance uniquely explained by that variable by subtracting the deviance of the model excluding that variable from the full model deviance. Variables explaining <0.1% deviance were retained in the final model, but deemed to have little biological significance.

A total of 87% of the dataset in this study was composed of juveniles. We hence assumed that integrating size into the modelling framework would have very limited power and could potentially lead to misleading results. To validate our assumption, we added FL as an explanatory variable to the final model and compared performances of both models based on change in deviance. To investigate whether different life stages of immature white sharks were impacted differently by the tested variables, we grouped sharks into young-of-the-year (total: n = 24; detected n = 10), sub-adults (total: n = 33; detected: n = 26) and juveniles (total: n = 387; detected: n = 303). To determine if differences in sample size influence model results, we also created a subset of 15 randomly sampled individuals of the juvenile group. We then ran all possible combinations of explanatory variables alongside the null model, calculated AICc values using the 'dredge' function for each of the 4 groups and ranked candidate models according to AICc and weight.

To test whether the observed response of white shark occurrence to time of day, water temperature, tidal height, swell height and lunar phase was driven by receiver performance, we fitted candidate models for the range test dataset and 4 subsets of the white shark occurrence dataset: (1) white shark presences during the range test period at range test receiver locations only; (2) white shark presences during the range test period at non-range test receiver locations only; (3) white shark presences during the range test period across all receiver locations; and (4) white shark presences across the 3 yr study period across all 19 receiver locations. We then visually compared their overlaid graphical outputs. Overlapping confidence intervals between range test and detection response curves represent the part of the gradient of each variable in which white shark occurrences were likely driven by receiver performance.

2.3.2. Model performance evaluation

To measure the predictive accuracy of the models, we used the area under the receiver operator characteristic curve (AUC) to evaluate performance of models in the 'PresenceAbsence' package in R (Freeman & Moisen 2008). AUC values designate the probability that positive and negative instances are correctly classified. The AUC ranges from 0.5 (equivalent to the prediction from a random model) to 1 (perfect predictions). Values of 0.5–0.69, 0.7–0.9 and >0.9 represent poor, reasonable and very good model performance, respectively. To ensure that model performance was not driven by a small number of individuals, we re-ran the entire model selection process, excluding 10 individuals that showed a disproportionately high number of detections (33% of total detections) (Fig. S4).

3. RESULTS

The 444 tagged sharks ranged in FL from 130–373 cm, with a mean ± SD of 228 ± 40 cm. Of those sharks, 60% were female, 87% were juveniles (155–280 cm FL; 227 female, 160 male), 7% were sub-adults (281–350 cm FL; 29 female, 4 male), and 5% were young-of-the-year sharks (130–155 cm FL; 10 male, 14 female) at the time of tagging. Eight sharks died between April 2017 and November 2019. Three of these were euthanized following capture as part of the Queensland Shark Control Program, 3 died in shark nets in the Sydney area as part of the NSW Shark Meshing Program, 1 washed up at a beach in Evans Head 5 d after tagging, and 1 was caught in the gummy shark fishery managed by the Australian Fisheries Management Authority in Victoria. Within the study period, all receivers operated continuously, yet due to technical issues, receivers at Kingscliff, Evans Head, Yamba, Port Macquarie, Kiama and Merimbula (Fig. 1) were not operative for different time periods ranging from 7 to 23 d between July and December 2018. All non-operative periods were excluded from the modelling framework.

3.1. Patterns of occurrence

Of the 444 tagged sharks, 339 individuals (76%) were detected by the VR4G receiver array a total of 42 509 times after removing double detection counts, including receivers at Ballina Lighthouse and Lennox Head (7818 after hourly binning) between 01 December 2016 and 30 November 2019 (Fig. 2). The largest number of sharks (n = 150) and detections (n = 2661) were recorded in Forster (Fig. 2). Overall, occupancy was highest between South West Rocks and Hawks Nest on the mid-NSW coast. The number of sharks tagged at a certain location did not directly correspond to the number of sharks detected by receivers adjacent to that location; e.g. no sharks were tagged adjacent to the South West Rocks receiver,

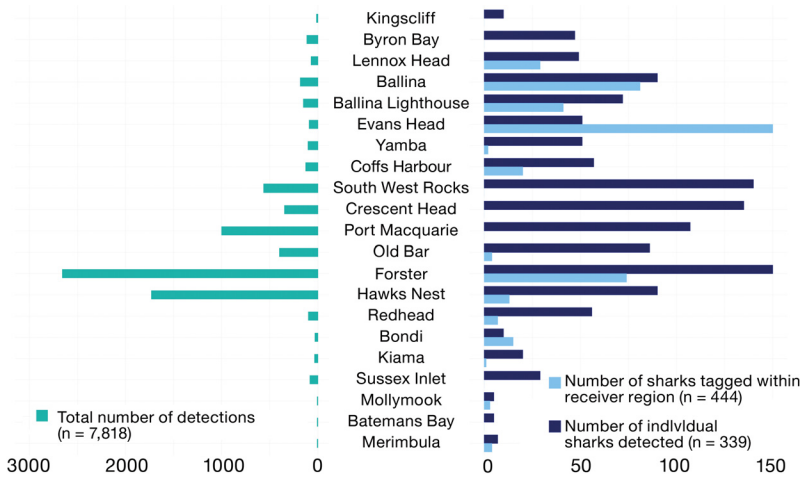

Fig. 2. Summary of total detections and tagged vs. detected immature white sharks by location, including numbers of (1) total detections (n = 7818, after hourly binning); (2) tagged immature white sharks (n = 444); and (3) individual sharks (n = 339) detected by receiver location between 01 December 2016 and 30 November 2019

yet this location showed the second highest number of detected animals (Fig. 2). Likewise, the total number of detections did not always directly correspond to the number of sharks detected; e.g. Hawks Nest recorded the second highest number of detections yet was only fifth in number of individual sharks detected (Fig. 2). This is due to extended detection periods of a very small number of sharks (Fig. S4). For example, 5 sharks accounted for 64% of the total detections by the Hawks Nest receiver. Similarly, 1 shark accounted for 21% of the total detections at the Forster receiver and 7% of the total number of detections across all locations. Pooled hourly binned detection data (across all receiver locations over the entire study period) indicated higher numbers of individual sharks detected during the day than at night-time (Fig. S5A). Detection data pooled over the 3 yr study period (01 December 2016 to 30 November 2019) and all receiver locations indicated a clear seasonality, with occurrences peaking in the austral spring (September–November) (Fig. S5B,C).

3.2. Drivers of occurrence

The final GAM chosen through the model selection process considered 386 224 observations of presence and absence over a 3 yr period and retained all candidate predictor variables (Table S5). The proportion of the variation in shark occurrence explained by the final model was 21%. Of these, 17.3% were attributed to the effect of receiver location (Table S6). Unique deviance explained ranged from 0.27–0.57% for month, time of day and swell height, and was <0.1% for water temperature, tidal height and lunar phase, indicating limited to negligible effects in the model (Table S6). Graphical output indicated a seasonal pattern of white shark occurrences, with a peak in September followed by a decline in individuals from October to April (Fig. 3). Sensitivity tests demonstrated that our approach of randomly sampling absences was robust. Changes in deviance among models based on the 5 resampled datasets were marginal (Table S7), and graphical outputs were virtually identical.

Model results also indicated higher shark numbers during the daytime, peaking at 11:00 h (Fig. 3). The relationship between water temperature and the presence of sharks highlighted a peak in shark occurrences for temperatures between 18 and 24°C. There was a negative linear relationship between the number of occurrences and swell height, with a decrease in occurrences with increasing swell height above 2 m. Occurrences were lower at low and high tide and peaked at full moon (Fig. 3). The ability of the final model to predict shark presence was considered 'reasonable' based on an AUC value of 0.87 (Table S5). Visual comparison between graphical

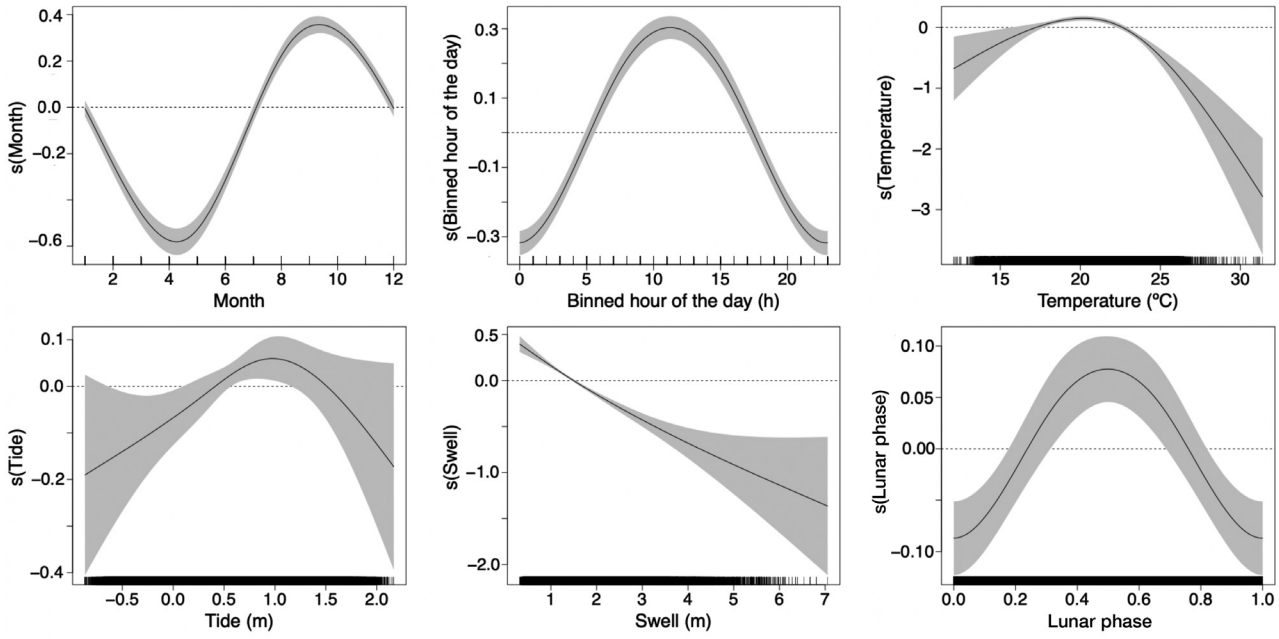

Fig. 3. Response curves of the 6 variables included in the most supported model predicting immature white shark occurrence along the coast of New South Wales, Australia. S(x): GAM smoother estimated for variable (x). Grey shading indicates 95% confidence limits. Positive values on the vertical axes indicate an increased probability of occurrence, while negative values indicate an increased probability of absence. Lunar phase values correspond to new moon (0), first quarter (0.25), full moon (0.5) and second quarter (0.75)

outputs of the full data set and the data set excluding the 10 most detected sharks did not indicate a significant difference in model performance (Fig. S6).

Size-based differences in occurrence patterns of the sharks tagged in this study could not be identified. Integration of the variable FL into the final model had no significant effect on shark occurrences and resulted in a decrease of deviance explained by the full model. GAMs separated by life stage indicated differences in the factors driving the occurrence of young-of-the-year, sub-adult and juvenile sharks. Young-of-the year sharks were driven by all variables except for tidal height, while only the variables month and time of day were retained for sub-adults (Table S8, Fig. S7). The final model chosen for juveniles retained all variables and had a graphical output that was identical to that of the full model including all life stages. The final GAM chosen for a subset of juveniles, however, retained only the variables month, time of day and swell height, indicating that model selection was influenced by sample size.

GAM response curves of receiver detection efficiency and white shark presence showed similar trends, with partially overlapping confidence intervals for the variables swell height and lunar phase across all white shark presence data subsets (Fig. S8). This suggests that observed occurrence patterns of white sharks were likely negatively biased by substantially reduced receiver performance with increasing swell height and lunar phase (from new to full moon). Shark detection response curves for the variables time of day, tidal height and water temperature showed only little overlap with receiver detection efficiency curves across all data subsets (Fig. S8). Within the temperature range observed during the range test period, shark detections decreased linearly from 16–23°C, whereas receiver performance showed an optimum between 17 and 20°C, followed by a drastic decrease in detection efficiency (Fig. S9). This indicates that shark detections above 20°C were strongly negatively influenced by receiver performance and are likely much higher than indicated by the model response curves (Fig. 3).

4. DISCUSSION

Rising impacts of anthropogenic stressors on marine predator populations have heightened the need to better understand the drivers of shark movements and occurrence patterns. We acoustically tagged an estimated 8–20% of the immature Australasian white shark population and demonstrate that environmental factors had little effect on the occurrence of these sharks along the NSW coast of Australia. The bulk of the total variation in detection data (~79%) remained unexplained by our model. Collectively, the variables month, time of day, water temperature, tidal height, swell height and lunar phase explained ~5% of deviance, while 17% were attributable to differences in receiver location. This variation probably relates to physical or biological characteristics of the adjacent or immediate receiver environment. Highly variable receiver performance somewhat complicated our occurrence analyses, but we were able to appropriately quantify variable detection efficiency through range tests at selected receivers. Receiver performance was likely influenced by both environmental conditions and biological noise, providing an example of how a lack of controls can lead to misinterpretation of shark occurrence patterns.

4.1. Environmental and temporal influences

While there is substantial evidence that abiotic factors can drive movements in sharks (see Schlaff et al. 2014 for a review), our results suggest that most variables assessed in this study had a limited effect on the presence of tracked sharks along the NSW coast of Australia. Month accounted for the largest amount of deviance of all factors for the GAM presented here, predicting strong seasonal variation, with most sharks occurring along the NSW coast between July and December. The predicted seasonality is consistent with previous work demonstrating highest abundances during the austral winter and spring (June–November) (Bruce et al. 2019, Spaet et al. 2020) and peak catch rates from September to November (Reid et al. 2011). The overall seasonal signal in movements suggests a response to an environmental cue, and several studies have linked the distribution of white sharks with water temperature (Dewar et al. 2004, Weng et al. 2007, Bruce & Bradford 2012, Weltz et al. 2013, Lee et al. 2018, Wintner & Kerwath 2018). Results of previous work modelling the effect of temperature on immature white shark occurrence on limited sample sizes, are inconsistent, identifying temperature as a predominant predictor of shifts in juvenile white shark distribution in the Southern California Bight (White et al. 2019) and as a poor predictor in the Port Stephens estuary in NSW (Harasti et al. 2017). We found that the deviance explained by temperature was only 17% of the deviance explained by the temporal factor 'month', suggesting that other environmental factors, not accounted for in this study, are

driving seasonal variation. For example, photoperiod (day length) strongly influences the migratory activity of many species (Milner-Gulland et al. 2011), including sharks (e.g. Grubbs et al. 2007, Dudgeon et al. 2013) and could be responsible for a large proportion of the variation associated with month. The limited effect of temperature encountered here is not surprising given that white sharks are endotherms and their behaviours and distributions are less likely to be influenced by thermal cues (Carey et al. 1982, Goldman 1997). Although temperature can also have indirect effects on white shark distribution by affecting prey distribution and abundance, based on the limited effect this factor had on the 444 sharks tracked in this study, temperature does not appear to be a robust predictor of immature white shark occurrences across regions.

While white sharks are known to undergo ontogenetic shifts in habitat, clear life-stage-based variation in occurrence patterns of the sharks tagged in this study could not be identified. Although GAM results differed between life-stage groups, this variation was likely influenced by sample size, as indicated by the differences in model results within the juvenile life-stage group, when the sample size was significantly reduced. Total detections of young-of-the-year and sub-adult sharks equalled <6%, while the remaining 94% comprised detections of juveniles. Given the observed differences in model results between the full juvenile dataset and a subset thereof, we believe that the available data on young-of-the-year and sub-adult sharks are insufficient to yield robust model predictions.

The effect of tidal height, which largely depends on the bottom topography of coastal areas, was negligible. Receiver sites in this study all have a gradually declining bathymetry and lack any sudden drop-off of the coastal shelf. Furthermore, the mean tidal range across all receiver locations was a modest 1.82 m. While some shark species have been observed to move closer inshore with incoming tides to exploit previously unattainable resources (Ackerman et al. 2000, Carlisle & Starr 2009), in our study, the amount of available habitat which increases or decreases with incoming or outgoing tide, respectively, is likely not substantial enough to affect the movement of tracked sharks.

4.2. Influence of receiver performance

The final GAM in our study suggested a thermal preference of immature white sharks in the eastern Australasian population of between 18 and 23°C. Yet, considering the dramatic negative effect of temperature on receiver performance above 20°C (see Text S1, Table S4 and Fig. S9), predicted presences above this threshold are likely substantially higher than indicated by our modelling framework. The limited range test data available for this study restrict our ability to statistically correct for variability of the environmental variables affecting receiver performance. However, based on a comparison of GAM response curves between range test and white shark detection data (Figs. S8 & S9), we estimated the upper limit of the predicted thermal preference to be 3–4°C above the limit indicated by the final GAM, so probably ranging from 18–27°C. This is consistent with the temperature preference reported in other studies for juvenile white sharks in the northeast Pacific, ranging from 17.5–25°C (Weng et al. 2007, Domeier & Nasby-Lucas 2008) and 19–26°C (White et al. 2019). An acoustic telemetry study of 20 juvenile white sharks in Port Stephens, a NSW estuary (adjacent to the VR4G receiver at Hawks Nest of this study), revealed a drastic decrease in detections of immature white shark at temperatures above 20°C (Harasti et al. 2017). The authors concluded that water temperatures were correlated with the presence of immature white sharks in the estuary, suggesting a thermal preference of 15–19°C (Harasti et al. 2017). However, potential effects of environmental variables on receiver performance were not assessed in that study. While it cannot be ruled out that the same detection patterns appear in animal and control tag detection data, the similarities between this previous work and the receiver performance results presented here (see Text S1, Table S4 and Figs. S8 & S9) might suggest that the temperature-related detection patterns observed by Harasti et al. (2017) were strongly influenced by receiver performance. This example highlights the critical importance of understanding receiver performance across variable environmental conditions (Kessel et al. 2014) and the need to distinguish between environmental interference and animal behaviour (Mathies et al. 2014). Based on the large number of sharks tracked in our study and the receiver performance results accompanying this manuscript (see Text S1), we suggest that the previously proposed propensity of immature Australasian white sharks to temperatures between 18 and 20°C (Bruce & Bradford 2012) likely extends up to 27°C in nearshore areas of the Australian east coast.

Receiver performance also strongly influenced occurrence patterns related to the variables swell height and lunar phase. GAM response curves for

both variables showed the largest overlap between receiver performance and white shark detection data. This suggests that the observed correlations between these variables and shark occurrences are a result of environmental interference, and do not reflect actual white shark behaviour (see Text S1 for a discussion on potential causes of reduced receiver performance during increased swell height and lunar phase). While diel patterns of shark presence appear to be less influenced by receiver performance, the general trend of increasing detection efficiency with time of day (from night to day) was similar for the shark detection and range test datasets (see Text S1 for a discussion on potential causes of reduced receiver performance during night-time). Satellite tracking studies investigating the vertical diving behaviour of immature white sharks in the east Pacific have reported strong diurnal dive patterns, with significantly deeper mean positions during daytime (Dewar et al. 2004, Weng et al. 2007, Domeier & Nasby-Lucas 2008). Diel-depth patterns of Australasian sharks appear to be weaker, ranging from strong to negligible, but with a general trend of occupying deeper habitats during the day (Bruce & Bradford 2012, Francis et al. 2012). If the sharks tracked in this study displayed diel dive-patterns similar to the ones previously described, we would expect a reduced likelihood of detection during the day, given that all receivers were deployed in shallow nearshore areas. This might indicate that diel patterns of shark occurrences are more strongly biased than indicated by our results. Hence, until further information of the acoustic properties of the water body at the time of detection is available, caution should be exercised in drawing conclusions about the observed diel patterns.

Our results should also be interpreted in relation to the design of the acoustic array. We deployed 21 receivers along a substantial stretch of coastline (~1000 km), resulting in limited coverage in proportion to the total study area (Fig. 1). Sampling design in acoustic surveys typically entails a trade-off between optimal coverage and the substantial costs involved with an increasing density of receivers (Clements et al. 2005, Heupel et al. 2006a). Here, the assessment of broad-scale environmental factors necessitated the large study scale. While electronic tag options (e.g. pop-up satellite archival tags) might have yielded a higher spatial resolution and more detailed patterns at this geographic scale, the deployment of several hundred electronic tags would not have been financially feasible. Our approach hence represents a compromise between geographic scale, sample size and spatial resolution. Overall, we believe that our design allows for general conclusions about space use in a vagile species, such as white sharks.

4.3. Potential location-specific factors

In this study, the largest proportion of variation in shark occurrence was explained by differences in receiver locations. Overall occurrences were highest between South West Rocks (30.88° S, 153.04° E) and Hawks Nest (32.40° S, 152.11° E) on the mid-coast of NSW. Using a combination of satellite and acoustic tracking data, recent research has suggested an ontogenetic range extension of the previously described 'Port Stephens nursery area' north- and southward, from Forster (32.18° S, 152.51° W) to south of Terrigal (33.44° S, 151.44° W) (Spaet et al. 2020). Based on abundance patterns in this study, we hypothesize a further northward expansion of the nursery area from Forster to South West Rocks. The ~300 km stretch of coastline between Terrigal and South West Rocks appears to represent a large 'nursery area', composed of a set of interconnected estuaries, bays and beach areas. Changes in temperature (Grubbs et al. 2007, Heupel et al. 2007, Yates et al. 2015), tidal conditions (Rechisky & Wetherbee 2003, Harasti et al. 2017) and lunar phase (Harasti et al. 2017) have previously been identified as likely drivers of shark abundance within nursery areas. The weak effects of these variables in our study indicate that other habitat-specific factors characteristic to the proposed, enlarged nursery area are the main drivers of immature white shark occurrences. The Port Stephens region, for example, harbours seasonal aggregations of various finfish species during periods of seasonal upwelling (Bruce & Bradford 2012). Additionally, chlorophyll *a* concentrations along the mid-NSW coast peak during October–November (Hallegraeff & Jeffrey 1993), the period during which most sharks were detected across all receiver locations (Fig. S5B). The predicted seasonal cycle of occupancy of this region (as opposed to antiquated theories of resident sharks at specific beaches) might hence suggest that the use of these habitats is associated with seasonal foraging opportunities provided by the local abundance of potential prey across the region. Information on biotic components and additional environmental data, such as prey availability, foraging success, stomach content data, local currents, physical structures, benthic cover, movement patterns of individuals and competition between individuals, were not considered in this study, but if re-

corded in the respective habitats, will likely increase the explanatory power of future analyses (Heithaus 2001, Heithaus et al. 2002, Torres et al. 2006). The incorporation of such data will also facilitate a better understanding of changes in spatial occurrence patterns associated with shifting environmental factors and/or prey resources (Navarro et al. 2016). Moreover, experimental approaches investigating relevant intrinsic (e.g. growth rates and mortality) and extrinsic (e.g. habitat quality) factors will help to elucidate the underlying mechanisms of habitat preferences and spatial distributions (Valavanis et al. 2008).

4.4. Implications for conservation

Immature white sharks are particularly susceptible to fishing activities, due to their relatively small size and their affinity to nearshore areas (Bruce & Bradford 2012, Lowe et al. 2012, Oñate-González et al. 2017). The mid-NSW coast is a populated region and an important tourist destination, rendering sharks vulnerable to interactions with recreational and commercial fisheries (Malcolm et al. 2001). While the unique functions provided by the proposed NSW nursery habitat remain to be elucidated, the results of this study suggest that future threat identification and mitigation for immature Australasian white sharks should focus on the area between South West Rocks and Hawks Nest. A better understanding of the factors driving habitat use patterns within this area will foster improved management practices, and facilitate the prediction of potential shifts in distribution associated with anthropogenic threats, such as coastal development or a changing climate.

Acknowledgements. Primary project funding and support was provided by the New South Wales Department of Primary Industries (NSW DPI) through the Shark Management Strategy. J.L.Y.S. received financial support through the German Academic Exchange Service (DAAD), NSW DPI and the Marine Ecology Research Centre, SCU. NSW DPI provided Scientific (Ref. P01/0059[A]), Marine Parks (Ref. P16/0145-1.1) and Animal Care and Ethics (ACEC Ref. 07/08) permits. Thank you to Barry Bruce, Russ Bradford (CSIRO) and David Harasti (NSW DPI) for providing catch details for 13 sharks tagged at Hawks Nest through a Marine Biodiversity Hub project, which is a collaborative partnership supported through funding from the Australian Government's National Environmental Science Program (NESP). We are grateful for infrastructure support provided by NSW DPI divers, various contracted divers and compliance officers for receiver maintenance. We also thank E. Fernando Cagua, Christopher Knox and Caitlin Frankish for advice on data organisation and analysis.

LITERATURE CITED

Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ Biol Fishes 58:33–43

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3: 327–338

Bartoń K (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bradford RW, Bruce BD, McAuley RB, Robinson G (2011) An evaluation of passive acoustic monitoring using satellite communication technology for near real-time detection of tagged marine animals. Open Fish Sci J 4:10–20

Bruce BD, Bradford RW (2012) Habitat use and spatial dynamics of juvenile white sharks, *Carcharodon carcharias*, in eastern Australia. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 225–254

Bruce BD, Stevens JD, Malcolm H (2006) Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. Mar Biol 150:161–172

Bruce BD, Harasti D, Lee K, Gallen C, Bradford R (2019) Broad-scale movements of juvenile white sharks *Carcharodon carcharias* in eastern Australia from acoustic and satellite telemetry. Mar Ecol Prog Ser 619:1–15

Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL Jr (1982) Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982:254–260

Carlisle AB, Starr RM (2009) Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Mar Ecol Prog Ser 380:213–228

Carlisle AB, Starr RM (2010) Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environ Biol Fishes 89:31–45

Certain G, Bellier E, Planque B, Bretagnolle V (2007) Characterising the temporal variability of the spatial distribution of animals: an application to seabirds at sea. Ecography 30:695–708

Chin A, Kyne PM (2007) Vulnerability of chondrichthyan fishes of the Great Barrier Reef to climate change. In: Johnson J, Marshall P (eds) Climate change and the Great Barrier Reef: a vulnerability assessment. Great Barrier Reef Marine Park Authority and Australian Green House Office, Townsville, p 394–425

Clay TA, Manica A, Ryan PG, Silk JRD, Croxall JP, Ireland L, Phillips RA (2016) Proximate drivers of spatial segregation in non-breeding albatrosses. Sci Rep 6:29932

Clements S, Jepsen D, Karnowski M, Schreck CB (2005) Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. N Am J Fish Manag 25:429–436

Department of Sustainability, Environment, Water, Population and Communities (2013) Recovery plan for the white shark (*Carcharodon carcharias*). DSEWPC, Canberra

Dewar H, Domeier M, Nasby-Lucas N (2004) Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. Environ Biol Fishes 70:133–143

Domeier ML, Nasby-Lucas N (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Mar Ecol Prog Ser 370:221–237

Dudgeon CL, Lanyon JM, Semmens JM (2013) Seasonality and site fidelity of the zebra shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. Anim Behav 85: 471–481

Francis MP, Duffy CAJ, Bonfil R, Manning MJ (2012) The third dimension: vertical habitat use by white sharks, *Carcharodon carcharias*. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 319–342

Frankish CK, Manica A, Phillips RA (2020) Effects of age on foraging behavior in two closely related albatross species. Mov Ecol 8:7

Freeman EA, Moisen G (2008) PresenceAbsence: an R package for presence absence analysis. J Stat Softw 23:1–31

Goldman KJ (1997) Regulation of body temperature in the white shark, *Carcharodon carcharias*. J Comp Physiol B 167:423–429

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50:87–107

Guyomard D, Perry C, Tournoux PU, Cliff G, Peddemors V, Jaquemet S (2019) An innovative fishing gear to enhance the release of non-target species in coastal shark-control programs: the SMART (shark management alert in real-time) drumline. Fish Res 216:6–17

Hallegraeff GM, Jeffrey SW (1993) Annually recurrent diatom blooms in spring along the New South Wales coast of Australia. Mar Freshw Res 44:325–334

Harasti D, Lee K, Bruce B, Gallen C, Bradford R (2017) Juvenile white sharks *Carcharodon carcharias* use estuarine environments in south-eastern Australia. Mar Biol 164:58

Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ Biol Fishes 61:25–36

Heithaus M, Dill L, Marshall G, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar Biol 140:237–248

Heupel MR, Semmens JM, Hobday AJ (2006a) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006b) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fishes 76:47–67

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Hillary RM, Bravington MV, Patterson TA, Grewe P and others (2018) Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. Sci Rep 8:2661

Huveneers C, Apps K, Becerril-García EE, Bruce B and others (2018) Future research directions on the 'elusive' white shark. Front Mar Sci 5:455

Jiménez-Valverde A, Lobo J, Hortal J (2009) The effect of prevalence and its interaction with sample size on the reliability of species distribution models. Community Ecol 10:196–205

Kelley D, Richards C (2020). oce: analysis of Oceanographic Data. R package version 1.2-0. https://CRAN.R-project.org/package=oce

Kessel ST, Cooke SJ, Heupel MR, Hussey NE and others (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24: 199–218

Lee KA, Roughan M, Harcourt RG, Peddemors VM (2018) Environmental correlates of relative abundance of potentially dangerous sharks in nearshore areas, southeastern Australia. Mar Ecol Prog Ser 599:157–179

Lindholm J, Auster PJ, Knight A (2007) Site fidelity and movement of adult Atlantic cod *Gadus morhua* at deep boulder reefs in the western Gulf of Maine, USA. Mar Ecol Prog Ser 342:239–247

Lowe CG, Blasius ME, Jarvis ET, Mason TJ, Goodmanlowe GD, O'Sullivan JB (2012) Historic fishery interactions with white sharks in the Southern California Bight. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 169–186

Malcolm H, Bruce BD, Stevens JD (2001) A review of the biology and status of white sharks in Australian waters. CSIRO Marine Research, Hobart

Mathies NH, Ogburn MB, McFall G, Fangman S (2014) Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. Mar Ecol Prog Ser 495:27–38

Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Mar Ecol Prog Ser 447:165–178

Medwin H, Clay CS (1997) Fundamentals of acoustical oceanography. Academic Press, New York, NY

Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) Animal migration: a synthesis. Oxford University Press, New York, NY

Mull CG, Lyons K, Blasius ME, Winkler C, O'Sullivan JB, Lowe CG (2013) Evidence of maternal offloading of organic contaminants in white sharks (*Carcharodon carcharias*). PLOS ONE 8:e62886

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059

Navarro J, Cardador L, Fernández ÁM, Bellido JM, Coll M (2016) Differences in the relative roles of environment, prey availability and human activity in the spatial distribution of two marine mesopredators living in highly exploited ecosystems. J Biogeogr 43:440–450

Oñate-González EC, Sosa-Nishizaki O, Herzka SZ, Lowe CG and others (2017) Importance of Bahia Sebastian Vizcaino as a nursery area for white sharks (*Carcharodon carcharias*) in the Northeastern Pacific: a fishery dependent analysis. Fish Res 188:125–137

Ortega LA, Heupel MR, Van Beynen P, Motta PJ (2009) Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environ Biol Fishes 84:361–373

Partridge L (1978) Habitat selection. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, p 351–376

Pyle P, Klimley AP, Anderson SD, Henderson RP (1996) Environmental factors affecting the occurrence and

behavior of white sharks at the Farallon Islands, California. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 281–291

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fishes 68:113–128

Reid DD, Robbins WD, Peddemors VM (2011) Decadal trends in shark catches and effort from the New South Wales, Australia, Shark Meshing Program 1950–2010. Mar Freshw Res 62:676–693

Rigby CL, Barreto R, Carlson J, Fernando D and others (2019) *Carcharodon carcharias*. The IUCN Red List of Threatened Species 2019: e.T3855A2878674

Robbins RL (2007) Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. J Fish Biol 70:1350–1364

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089–1103

Southall EJ, Sims DW, Witt MJ, Metcalfe JD (2006) Seasonal space-use estimates of basking sharks in relation to protection and political–economic zones in the North-east Atlantic. Biol Conserv 132:33–39

Spaet JLY, Patterson TA, Bradford RW, Butcher PA (2020) Spatiotemporal distribution patterns of immature Australasian white sharks (*Carcharodon carcharias*). Sci Rep 10:10169

Suchanek TH (1994) Temperate coastal marine communities: biodiversity and threats. Am Zool 34:100–114

Tate RD, Cullis BR, Smith SDA, Kelaher BP and others (2019) The acute physiological status of white sharks (*Carcharodon carcharias*) exhibits minimal variation after capture on SMART drumlines. Conserv Physiol 7:coz042

Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia 569:449–455

Towner AV, Underhill LG, Jewell OJD, Smale MJ (2013) Environmental influences on the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. PLOS ONE 8:e71197

Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Mar Ecol Prog Ser 480:171–183

Valavanis VD, Pierce GJ, Zuur AF, Palialexis A, Saveliev A, Katara I, Wang J (2008) Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. Hydrobiologia 612:5–20

Weltz K, Kock AA, Winker H, Attwood C, Sikweyiya M (2013) The influence of environmental variables on the presence of white sharks, *Carcharodon carcharias* at two popular Cape Town bathing beaches: a generalized additive mixed model. PLOS ONE 8:e68554

Weng KC, O'Sullivan JB, Lowe CG, Winkler CE, Dewar H, Block BA (2007) Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. Mar Ecol Prog Ser 338:211–224

Werry JM, Bruce BD, Sumpton W, Reid D, Mayer DG (2012) Beach areas used by juvenile white sharks, *Carcharodon carcharias*, in eastern Australia. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 271–286

Werry JM, Sumpton W, Otway NM, Lee SY, Haig JA, Mayer DG (2018) Rainfall and sea surface temperature: key drivers for occurrence of bull shark, *Carcharhinus leucas*, in beach areas. Glob Ecol Conserv 15:e00430

White CF, Lyons K, Jorgensen SJ, O'Sullivan J, Winkler C, Weng KC, Lowe CG (2019) Quantifying habitat selection and variability in habitat suitability for juvenile white sharks. PLOS ONE 14:e0214642

Wintner SP, Kerwath SE (2018) Cold fins, murky waters and the moon: What affects shark catches in the bather-protection program of KwaZulu–Natal, South Africa? Mar Freshw Res 69:167–177

Wood SN (2017) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, FL

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Ecological drivers of shark distributions along a tropical coastline. PLOS ONE 10:e0121346

Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA
Reviewed by: 3 anonymous referees

Submitted: June 9, 2020
Accepted: September 3, 2020
Proofs received from author(s): October 23, 2020